STUDIES IN PLATANACEAE.

By

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(With 4 plates).

The present investigation has been executed in the Botanical Laboratory at Utrecht at the suggestion of Professor A. Pulle. The intention was to investigate the general life-history, the development and the anatomy of the inflorescence and the flowers and the fertilization of the Platanaceae. Researches on this subject were of great interest because R. von Wettstein in his "Handbuch der systematischen Botanik" has given a leading systematical place to the Platanaceae on account of the very old typus which they seem to represent.

The intention of this communication is only to give a brief statement of methods and of the principal results of the investigation; more extensive accounts are contained in my dissertation titled "Onderzoekingen over de Platanaceae", which has been published in July 1923 and is illustrated by 86 figures.

Methods.

The material was obtained from ten trees, representing two types, which may be distinguished as Platanus orientalis and Platanus occidentalis, although both of them probably are only bastards. The material was collected weekly at Utrecht from February till October 1921, it was fixed in Fleming's and Juel's solutions and in mercurio chloride and picric acid according to Plowman's method. Because

of the early lignification of the hairy inflorescences only the last method proved to be satisfactory and for the same reason the material was imbedded by means of clove-oil into a mixture of paraffine and celloidine. Preparations were stained with Heidenhain's iron-hematoxylin and De Groot's iron-carmalaun. Series of sections were made with Minot's Reise-Microtom. Some microphoto's and drawings will be found at the end of this communication.

The General Life-History.

The Platanaceae are represented by the genus Platanus, which includes two species, P. occidentalis and P. orientalis. The difference between both only consists in the form of the leaves and the inflorescences, the former being resp. three-lobed and consisting of two balls, the latter being resp. five-lobed and consisting of three or four balls. A great many bastards between these two species with various transitory forms of leaves and inflorescences exist.

The habitus of the tree is peculiar on account of the macerated peduncles with the fruit-balls round the periphery as well as on account of the partly naked trunk. The habitus however varies with the seasons.

In winter the brown spirally inserted buds are entirely enclosed in the bases of the petioles. At the end of the branches the fruitballs are attached only by means of the fibres of their peduncles; the small bigheaded fruits form a close roof round each ball and under this roof a great many hairs are inserted between the fruits.

As soon as spring sets in, the buds begin to open in the same succession in which they were developed from the very beginning. First of all the topbud of the top-shoots of the lowest branches burst open, then this process is continued inward and upward on the branches, so that the contents of the buds are very slowly exposed to the

air. The leaves and their stipulae are densely haired and the young inflorescences in the buds are covered by a roof of green staminaheads under which the young carpellae are protected between a great many long hairs.

When the buds are opened, the inflorescences are stretched and the red styles of the carpellae are piercing through the roof of staminaheads. The ripe fruits are falling down from the balls, but they only germinate after some days floating vertically near the surface of the water. The basal regular circle of long straight hairs seems to keep them vertical when floating, and the big head being very loosely built seems to keep them floating quite under the surface of the water. If they remain a long time on the bottom of the water, they will be rotten. So it may be expected, that the fruits usually fall into a stream and after some days floating germinate on the moist shores of the stream.

In the last warm days of spring the loculamenti of the stamina burst open and the long red styles have a fresh sharp scent of moist leaves. Mosquito's are the only insects attracted by the inflorescence especially at this time of the year and they have been observed resting upon it for a considerable period. That they have something to do with the pollinisation may not be quite improbable. The pollen does not contain any starch.

The cotyledones of the seedlings are very often united at their bases. The form of the first leaves of the seedlings is remarkable because the first pair of lobes are only formed in the seventh leaf and the second pair of lobes of the P. orientalis-leaf only in the thirteenth leaf. So the tenth, eleventh and twelfth leaf of P. orientalis has the same form as the leaves of P. occidentalis. The hypocotyl of the young seedling is redcoloured when the temperature is low. Of great interest is the fact that this hypocotyl and the style of the carpellum are the only redcoloured

organs of Platanus, which are not hairy, and can be exposed to severe frosts in spring. The red colour of both organs disappears readily when the temperature rises, but it is very intense in times of frost; both organs are able to withstand frost perfectly.

At the beginning of summer all the fruits of the tree set very rapidly and all at once without any exception, before fertilization can have taken place. At this time the hairs of the leaves are shed.

At the end of summer the bark is beginning to be shed.

Immediately after the first frost-night in autumn the peduncles of the fruit-balls are partly macerated in the open air within a few hours time, so that only the extremely tough flexible fibres remain. Thus the fruit-balls are attached to the tree in an unique way during the whole winter. The leaves are all shed and the young buds are exposed to the air.

The inflorescence and the flowers.

The inflorescence of Platanus consists of a peduncle and two, three or four balls densely covered with groups of carpellae, stamina and hairs. This inflorescence is however characterised by the facts, that the stage of development of all the balls is the same and that the so-called peduncle only attaches the balls to each other (fig. 4).

The inflorescence is formed on the top of the young shoot in the bud as a single ball (fig. 3 at the right, fig. 20 at the left). On the surface of this ball stamina and carpellae are developing all in the same tempo, the ball itself consists of large cells and special food-cells and ten vascular bundles are supplying the ball. These bundles enter the ball in a circle (fig. 5), at the bottom of the ball five bifurcations of the bundles are found (fig. 6), the other five bundles, alternating with the first five bundles, reach the

top of the ball (fig. 7) and are bifurcated there (fig. 8). So the original ten bundles form twenty bundles which run to the periphery of the ball and from which issue rows of single bundles. Each single bundle supplies a stamen and a carpellum and is bifurcated just under the bases of these two organs, which entirely belong together.

Consequently the ball is covered by twenty rows of stamina and carpellae, twenty rows of paired organs. In these rows the pairs are spirally orientated, the result of which is that the pairs are alternately turning another side to those in the next rows. So groups of pairs are formed, in which the carpellae of various rows are surrounded by their resp. stamina. The number of pairs in these groups varies from three to nine, because the rows do not run quite straight; the components of the groups however are not really connected with each other, the pairs always belong to different rows (fig. 22).

These groups of carpellae are very misleading when the deeper construction of the ball is not known, indeed they have always been interpreted as flowers. In fact they are only the result of the spiral orientation of the pairs in the rows, which form the real construction of the ball (fig. 21).

This single young ball now is going to form two, three or four lobes, spirally orientated round the ball, and at last forming two, three or four new balls spirally orientated round each other (fig. 20 and fig. 3 at the left).

When the inflorescence leaves the bud and is stretched, the bases of the balls are growing. As all the organs on the various balls are already formed at this time, their orientation being already definitively determined on the single ball, these bases remain naked and slender. These bases of the balls form together the „peduncle" which unites the various balls and is only a false peduncle. The vascular bundles run in this peduncle from one ball into the other ball (fig. 20 and fig. 4).

By the way of development of the inflorescence it will be clear, why all the balls are always in the same stage of development. They are only parts of one single ball.

In fig. 9 and 10 the misleading orientation of the organs in the groups will be seen. The first section shows six carpellae and three stamina apparently forming three alternating circles; the second section shows their insertion, they form one spiral. Between the three stamina are alternating three short staminodia, the seventh carpellum is very short too and its stamen is suppressed. Round the group is scale, which is continuous however between all the groups (fig. 12), and has no vascular supply. This scale is only to be regarded as a proliferation of the ball. Under the groups the ball forms coni, round which the pairs are inserted in one spiral (fig. 4 and 10).

The real construction of the balls is to be observed when the fruits are ripe. On the fruit-balls (fig. 1 and 2) ten fields are to be distinguished, in which the length of the fruits increases centripetally. These ten fields represent the ten vascular bundles which enter the ball, the ten pairs of rows.

The paired stamen and carpellum in the rows belong together morphologically and biologically, for their bases are united, they have the same vascular supply, and the young carpellum is protected by the head of the stamen. In some cases both organs are united in such a way that is gives the impression that the stamen is bearing an ovulum. (B. Clarke).

The spiral insertion of the pairs in the rows implies that they might be in some way be compared with the leaves which are likewise orientated. It is especially the carpellum which might be compared with a leaf. Both leaf and carpellum have their margins folded backward when young, both have five vascular bundles which meet each other at the top, the carpellum consists of extremely

small cells sharply contrasting with the cells of the ball. The margins of the carpellum are united at the base, there forming a very small ovarium with one or two ovula taking their origin from the united margins. If the margins are not united no ovula are formed so they seem to be connected with the proliferation (Selmar Schönland). So the carpellum might perhaps represent a kind of fertilised dwarf-leaf, the balls representing the form of utmost compression. The front of the carpellum is turned to the stamen, so that the pollen cannot reach the style-canal between the backfolded margins. The top of the red style is turned away from the stamen.

The stamen consists of the same large cells and characteristic food-cells as the ball and it has a big head, which protects the young carpellum. Under this head four loculamenti are formed when the stamen is fertilised but in a great many cases this organ remains quite sterile, the vascular supply remaining intact. Therefore the stamen might be compared with a protective scale of the ball, meant to protect the carpellum and secondarily fertilised.

The ball with its covering of paired organs in rows, scales above fertilised leaves, indeed has some resemblance to the conus of Gymnosperms.

Two sorts of food-cells can be distinguished in the ball, some of them contain a great many oildrops, the other ones a great number of small starchgrains enveloped by a curious thin bag only visible after fixation with Flemings solution, so that it probably consists of some fatty substance round the starchgrains.

By the extremely dense insertion of the organs on the balls a great many stamina are suppressed or have become staminodial. In the groups the stamina usually are alternatively reduced. There are however entirely sterile stamina too, which may not be called staminodia because in a great many cases the ball is only covered by these

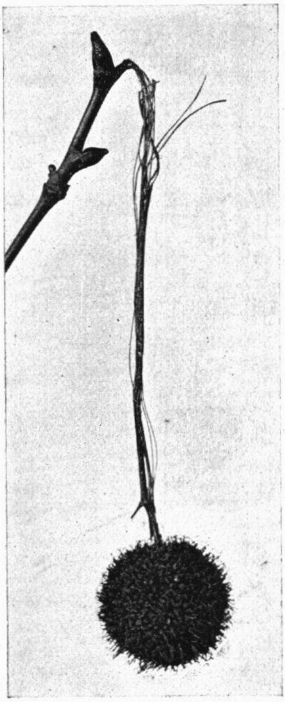
sterile organs and carpellae, thus being exclusively feminine. It is for this reason that I called these sterile organs scales. Other balls have lost their carpellae and therefore are exclusively masculine. It is very curious to see that this localisation of the sexes is very constant because the ♂ balls are only found at the end of the shoots, the ♀ balls being located behind the ♂ balls. This localisation is a rule without exception, but yet it cannot be primary, because it is obvious that the organs are originally meant to be paired.

The Fertilization.

As a matter of fact the fertilization has not been observed, so that only the development of the embryosac and the pollengrains will be described here. There are a few hints as to the abnormal forming of an embryo, but very minute investigations have still to be made on this point, the material for which has already been collected.

The development of the microspores is quite normal. The two tetrad divisions occur almost simultaneously, sixteen being the diploid number of chromosomes, this number is reduced to eight. Before the tetrad divisions the nuclei of the tapetum divide without forming cell-walls. The mature pollengrain has the form of a spheroid and a smooth surface. Soon after the pollengrain is freed from the mothercell its nucleus divides; the generative nucleus is dense and deeply staining, the vegetative nucleus is loosely vesicular.

When the pollengrains are nearly mature the ovulum is not yet differentiated, only when the buds are opened the archespore is distinguishable and the integuments are developed. Only the inner integument reaches the top of the nucellus enclosing a few nucelluscells in the micropyle. As a result of the tetrad devision a row of four cells



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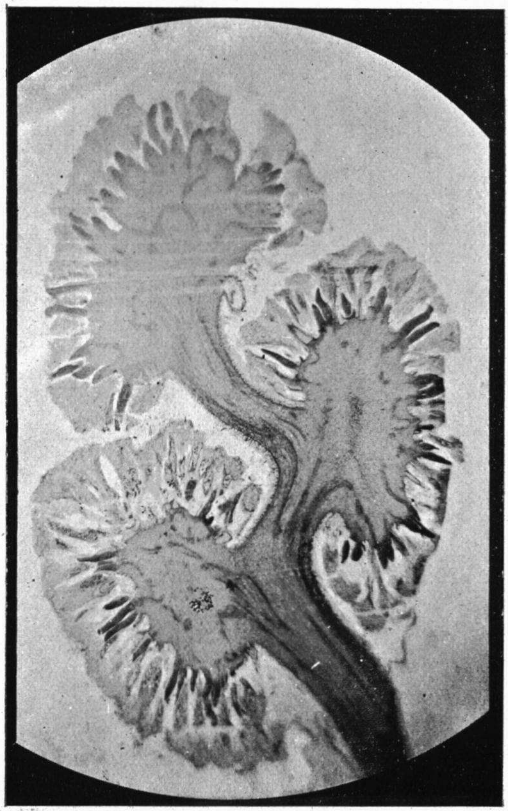

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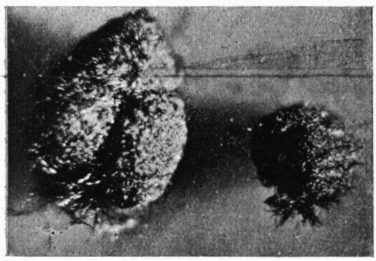

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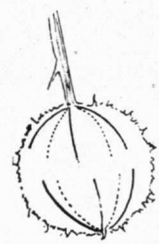

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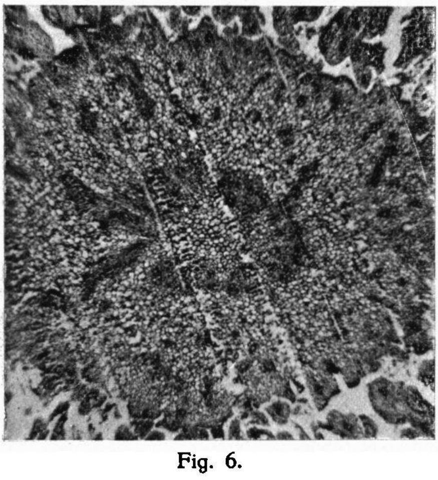

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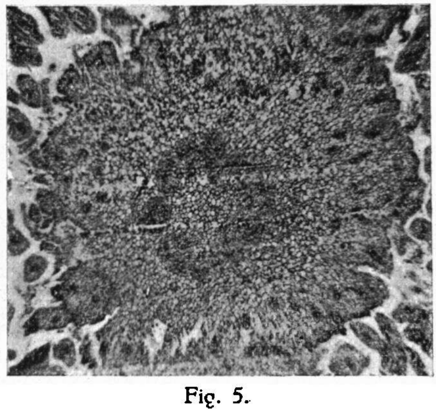

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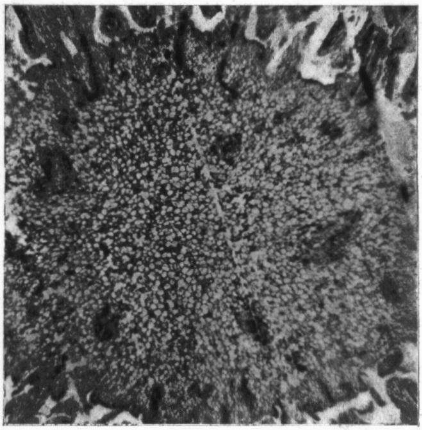

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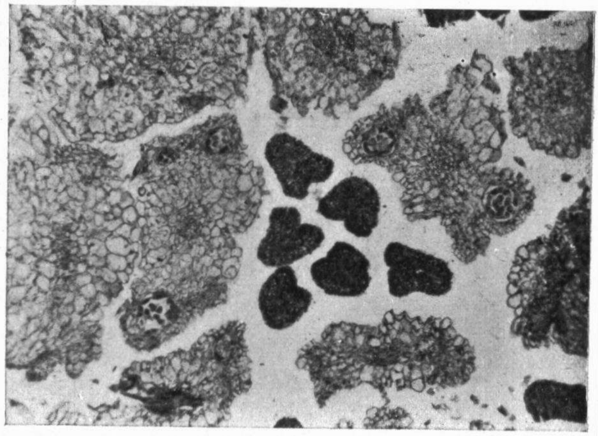

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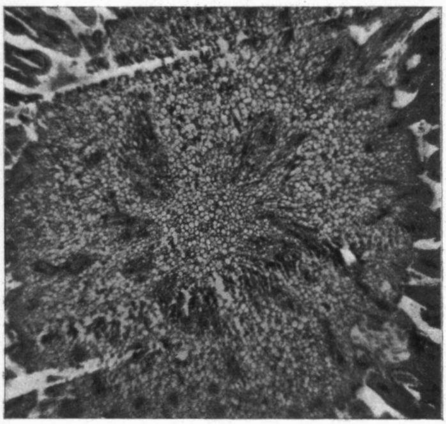

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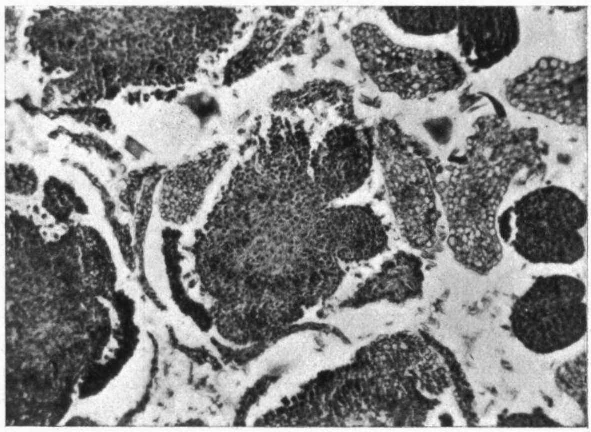

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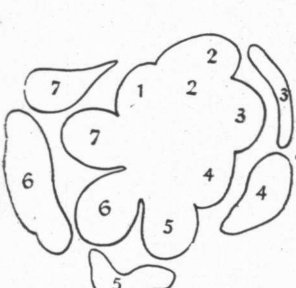


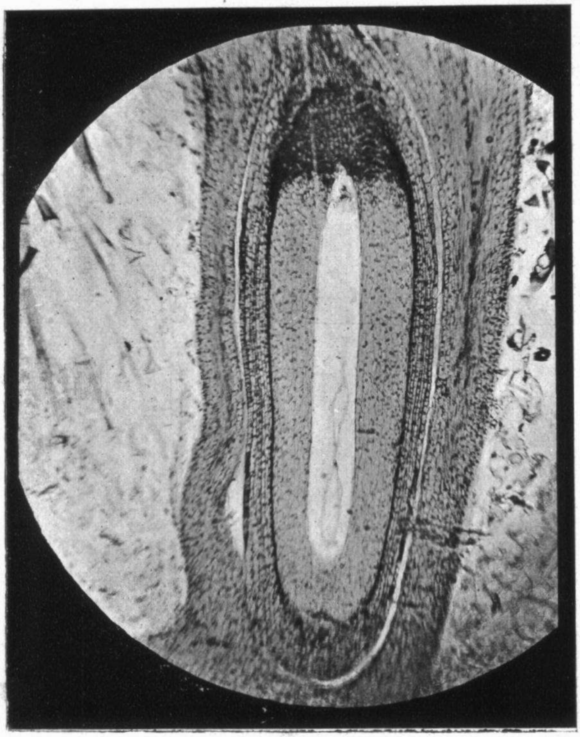
Fig. 11.

Fig. 12.

Fig. 13.

Fig. 15.

Fig. 14.



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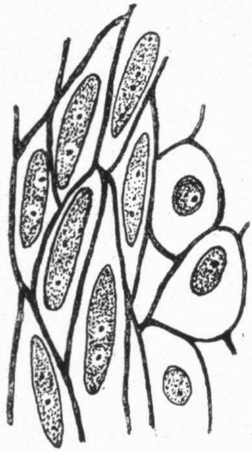

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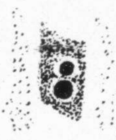

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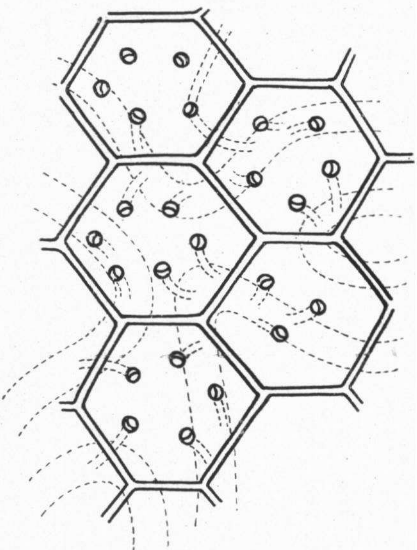

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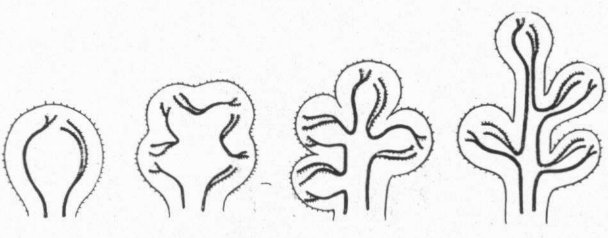
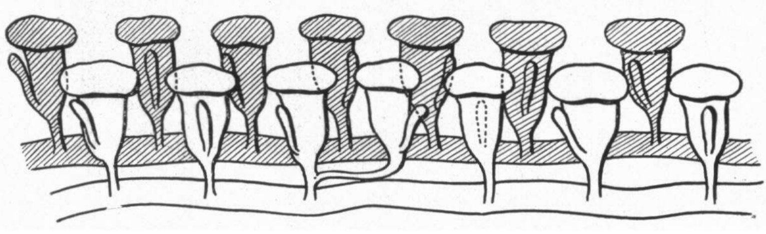


Fig. 20.

Fig. 21.



may be seen, the inmost cell only survives. Further divisions of the nucleus of this young embryosac are still occurring when pollinisation takes place and the pollen is falling on the stigma and sinks into the papillae of the stigma.

On the stigma the pollengrains do not sprout however as far as can be observed.

In order to test the nature of the pollen the pollengrains were laid on various sugar-solutions (1 to 30 %) in agar and gelatine and it was proved that the pollen sprouted very readily on every solution and even on water. When the pollengrains had sunk too deep into the solution the tubes grew out of the solution into the moist air. Very remarkable was it however that the pollengrains never sprouted on pieces of the stigmata laid in the solution, nor did they sprout on the extract of stigmata mixed with the solution.

Before and after the time of pollinisation the pollen could not be induced to sprout, so that after pollinisationtime (a few weeks) no fertilization is possible. When pollinisation is entirely done the embryosac is not yet fullgrown.

The behaviour of the nuclei in the pollentubes is normal. The generative nucleus enters first into the tube, it is followed by the vegetative nucleus, then the latter passes the former and disappears when the former divides.

After pollinisation the fruits set rapidly, the styles are dried up, the fruitwalls are lignificated, around the chalazal end of the embryosac the tissue always stains deeply. At this time the embryosac contains a small egg apparatus, three small antipodals and two big pole cells.

When the fruits are set the embryosac at last has reached its full length, but the egg apparatus and the antipodals have disappeared. The polar cells have fused however and form together one huge cell in the middle of the embryosac (fig. 16 and 17). This large cell is the only

survivor in the sac. Round the embryosac all the tissue has remained intact; immediately round the embryosac is a single layer of small flat cells with long nuclei, this layer is always intact too (fig. 18).

Now although no fertilization occurred, as far as could be observed, in the next stage large endospermcells are found in the embryosac and in the middle of the sac a very small row of two or three thin cells seem to be the very beginning of an embryo (fig. 19). The development of the embryo could not yet be observed however; only it was established at the end of summer that all the fruits of that year contained an embryo.

The exact behaviour of the polar cells after their fusion has yet to be investigated.

Discussion.

The systematic place of the Platanaceae has always been incertain on account of the irregularity of the flowers, as the groups of stamina and carpellae on the balls were called. Of course as the inner construction of the ball and the insertion of the organs was not known no reason could be found for the varying number of organs in the groups.

On account of the density of the inflorescence some systematici, as John Lindley and De Candolle placed the Platanaceae among the Urticales. B. Clarke called the staminodia a perianth and for this reason Le Maout et Decaisne and Baillon placed the Platanaceae among the Rosales. Selmar Schönland examined the Platanaceae very carefully in 1883, but the result was only a theoretical diagram of a complete flower consisting of six carpellae, six stamina, six petala and six sepala. In fact the six stamina and six petala are represented by three stamina and three staminodia only, the

remaining three stamina and three staminodia (petala) being the result of a false presumption. The sepala are represented by the continuous scale between the groups. So this diagram was an error, unfortunately it was however the cause that the Platanaceae were placed among the Rosales by F. M. Niedenzu in Engler and Prantl's „Die natürlichen Pflanzenfamilien", although Robert F. Griggs had declared in 1909 the flower of Platanus to be apetalous.

Indeed if there is any part in the inflorescence of the Platanaceae which might be called a flower it is the pair of organs, the united carpellum and stamen. Of course this flower is an extremely simple one.

The simplicity of this flower makes the opinion of R. Wettstein very interesting, as this author places the Platanaceae at the very beginning of the Angiospermae only on account of their general characters. In his system all the Dicotyledonae and Monocotyledonae are derived from this type and of course this unknown flower was meant to be simple.

The Platanaceae indeed have an entirely isolated position among Angiosperms, as well on account of their special foliar rays system (Bailey) as on account of the course of the vascular bundles in their petioles (Louis Petit) and their leaf fall (E. Lee). This has been clearly proved in comparative investigations of Angiosperms.

The fertilization of the Platanaceae has been investigated by Selmar Schönland and M. Th. Nicoloff; they could not find any trace of a pollentube either.

EXPLANATION OF PLATES.

Fig. 1. Fruitball. × $\frac{1}{2}$.
Fig. 2. The ten fields on the fruitball. × $\frac{1}{2}$.
Fig. 3. Two young inflorescences, at the right one single ball, at the left three balls. × 3.
Fig. 4. Longitudinal section through a young inflorescence. × 25.
Fig. 5. Cross-section through the bottom of a ball, ten vascular bundles entering the ball. × 25.
Fig. 6. Cross-section through the bottom of a ball, the bifurcation of one of the ten vascular bundles. × 25.
Fig. 7. Cross-section through the middle of the ball, five vascular bundles running to the top of the ball. × 25.
Fig. 8. Cross-section through the top of the ball, the bifurcation of the five vascular bundles. × 25.
Fig. 9. Cross-section through one of the groups consisting of six carpellae and three stamina. × 70.
Fig. 10. Cross-section through the same group as in fig. 9 at their insertion, seven carpellae and three stamina alternating with three staminodia forming one spiral, × 70.
Fig. 11. Drawing of fig. 10.
Fig. 12. The continuous scale between the groups. × 15.
Fig. 13. The hairs of the inflorescence with basal food-cells. × 70.
Fig. 14. Longitudinal seciion through a young stamen. × 125.
Fig. 15. Three branches in pollinisation-time. In the bottom branch the fruits are beginning to set. × $\frac{1}{2}$.
Fig. 16. Longitudinal section through the mature embryosac with fused pole cells in the middle. × 45.
Fig. 17. The fused pole cells. × 440.
Fig. 18. The cells of the single layer around the embryosac. × 440,
Fig. 19. The young embryo? × 440.
Fig. 20. The development of the inflorescence. Scheme. Two of the ten vascular bundles.
Fig. 21. Two rows of pairs, each pair consists of a bigheaded stamen and a very small carpellum. Two vascular bundles under the rows. Schematically.
Fig. 22. The transparent surface of the inflorescence. In the hexagonal fields the scars of the pairs above the vascular bundles. Scheme.

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